PROTOCYTIDIUM GEN. NOV., A NEW ANOMALOCYSTITID MITRATE FROM THE VICTORIAN LATEST ORDOVICIAN AND EVOLUTION OF THE ALLANICYTIDIIDAE

MARCELLO RUTA AND PETER A. JELL

The anomalocystitid mitrate *Protocytidium elliottae* gen. et sp. nov. is described from the uppermost Ordovician Darraweit Guim Mudstone in central Victoria. *Protocytidium* has: 1) 12 plates on the convex surface, with only 3 in distal row and the remaining 9 as in *Enoploura*; 2) remarkably asymmetrical lateral and median orifice plates of plano-concave surface divided into a 'thecal' portion framing the body orifice and a 'lip' projected distally beyond the orifice; 3) much reduced plate B failing to contact right LOP; 4) narrow, elongate plate A sutured with proximal 2/3-3/4 of medial margin of left intermediate lateral marginal plates; 5) short, slender, almost straight left spine and longer, more robust, convex, sickle-shaped right spine; 6) cancellate to honeycomb-like stereom, often replaced by radiating trabeculae near periphery of plates; 7) styloid trapezoidal, bearing semicircular styloid blades with radiating trabeculae; 8) proximal blade about half as large as distal blade. *Protocytidium* is intermediate between *Enoploura popei* and the basal allanicytidiid *Occultocystis koeneni*. The Allanicytidiidae are reviewed in the light of this new find. □ *Protocytidium, Anomalocystitida, Allanicytidiidae, Bolindian, Victoria.*

Marcello Ruta, Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom; Peter A. Jell, Queensland Museum, P.O. Box 3300, South Brisbane 4101, Australia; 10 June 1998.

During field mapping of the Kilmore 1:50,000 sheet (Vandenberg, 1992), which included a study of Ordovician/Silurian boundary sections in the Deep Creek and Ben Dhui Creek areas (Vandenberg et al., 1984), numerous specimens of a small mitrate were discovered at NMVPL660 in Ben Dhui Creek (Vandenberg et al., 1984, figs 1, 2A). This species has a combination of skeletal features making it transitional between *Enoploura* Wetherby, 1879 from the Middle to Late Ordovician of North America (Caster, 1952; Parsley, 1991) and the allanicytidiid *Occultocystis koeneni* Haude, 1995 from the Lower Devonian of Argentina. The new taxon is the oldest and only Ordovician member of the Allanicytidiidae. In this paper we describe and reconstruct the taxon, assess its phylogenetic position and discuss its bearing on the origin and evolution of the Allanicytidiidae.

GEOLOGICAL SETTING

The material described herein comes from NMVPL660 (Vandenberg et al., 1984, fig. 2A, appendix 2). It is in the bed of Ben Dhui Creek, 750m N of the Wallan to Woodend road, about 10km W of Wallan at AMG311740-5860360 on the Kilmore 1:50,000 sheet 7823-II Series R 754, Edition 1-AAS (1979). It is in the type section of the Darraweit Guim Mudstone which consists of medium to thick bedded massive calcareous mudstone. The mudstone is black when fresh but surface exposures are usually decalcified, weathered and grey or green as at NMVPL660. The associated fauna, which is preserved in situ, includes the trilobite *Songxites darraweitensis* (Campbell), the graptolite *Climacograptus angustus* Perner and nautiloids. This is a thin unit (20m in the type section) precisely dated by the widespread graptolite *Climacograptus? extraordinarius* (Soboleyskaya) which occurs in the youngest Ordovician Zone at the top of the Bolindian Stage.

SYSTEMATIC PALAEONTOLOGY

Anatomical terminology and plate nomenclature (Appendix) follow Ruta (in press), Ruta & Bartels (1998, fig. 5A,B) and Ruta & Jell (1999a,b,c). Specimens are housed in the Museum of Victoria, Melbourne (NMVP) wherein the locality is also registered (NMVPL). All photographic illustrations are of latex casts taken from decalcified moulds and whitened with ammonium chloride sublimate.
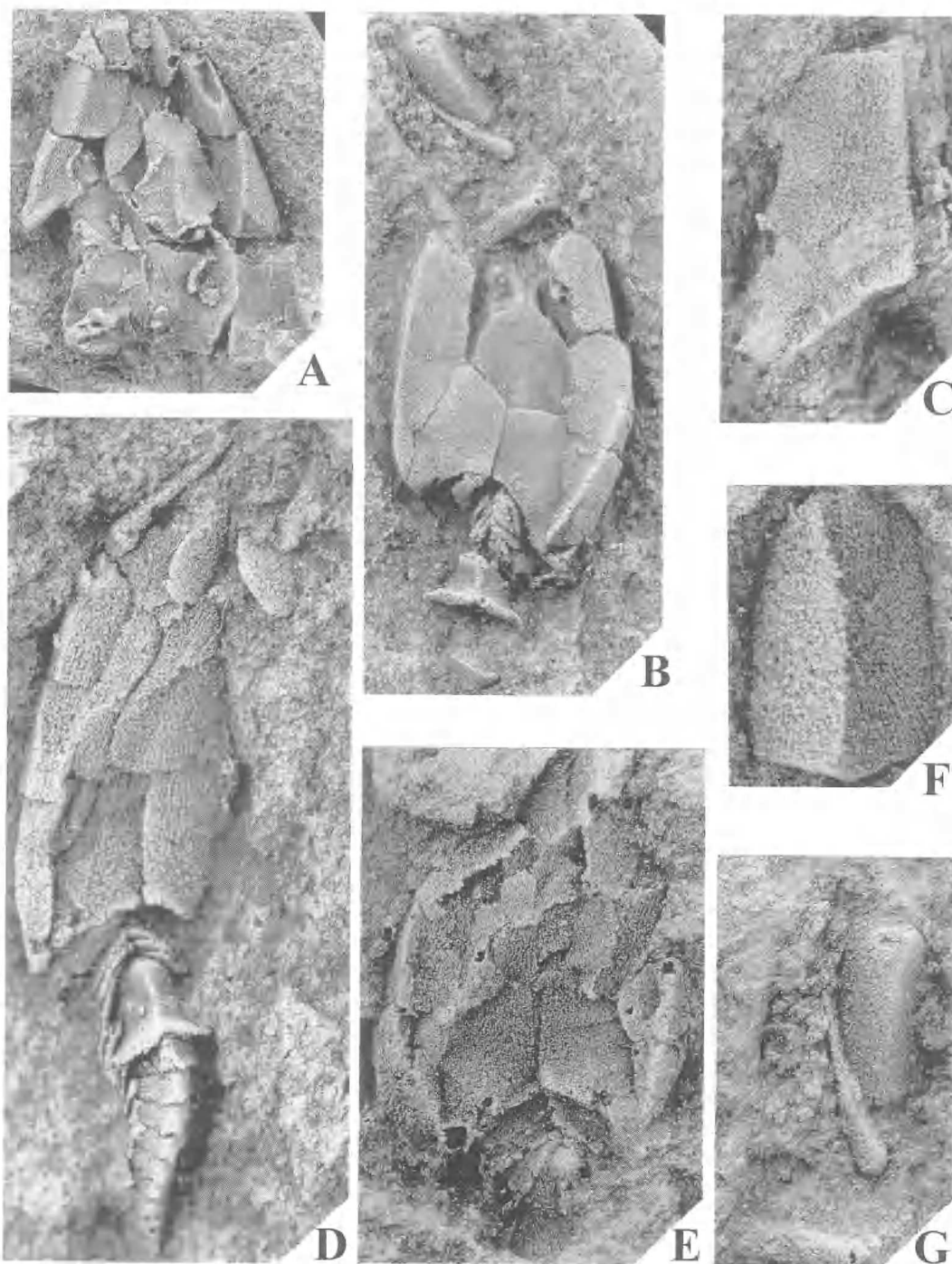
FIG. 1. *Protocytidium elliottae* gen. et sp. nov. A, inside of proximal part of convex surface and distal part of plano-concave surface of NMVP100439, ×5. B, G, partial plano-concave surface and detail of adjacent isolated spine (probably right spine) of NMVP100424, ×5 and ×7, respectively. C, fragment of marginal plate from plano-concave surface showing stereom fabric, NMVP100405, ×11. D, partial plano-concave surface and appendage, NMVP100401, ×5.5. E, partial plano-concave surface of NMVP100415, ×9. F, fragment of marginal plate from plano-concave surface showing stereom fabric, NMVP100400, ×11.

Class STYLOPHORA Gill & Caster, 1960
Order MITRATA Jaekel, 1918
Suborder ANOMALOCYSTITIDA
Caster, 1952
Family ALLANICYTIDIIDAE
Caster & Gill, 1967

DIAGNOSIS (modified from Caster & Gill, 1967; Caster, 1983; Haude, 1995; Ruta, in press). Median orifice plate (MOP) longer than each lateral orifice plate (LOP). Spines longer than distal margin of plano-concave surface. Distal part of convex surface of 3 or, more frequently, 2 plates with transverse thickening along inside of their distal margins. Distal styloid blade inclined proximally, sometimes with lateral ear-like projections. Sharp, longitudinal keel on external surface of styloid, failing to reach free margin of proximal blade (only in basal allanicytidiids). Proximal blade semicircular.

REMARKS. Ruta (in press) amended and expanded the diagnosis of the Allanicytidiidae, formalising Haude's (1995) proposal to include *Occultocystis koeneni*. As discussed below, some characters supporting the sister-group relationship between the new anomalocystitid and the Allanicytidiidae sensu Haude (1995) are diagnostic of the latter (Ruta, in press). Our diagnosis is, therefore, more generalised than those of Haude (1995) and Ruta (in press) and aims to avoid the problem of defining the Allanicytidiidae mainly on the basis of the simplified plating of the convex surface in the most derived representatives of the group (Caster, 1956, 1983; Caster & Gill, 1967; Philip, 1981; Ruta & Theron, 1997; Ruta & Jell, 1999c). However, reversal of some of the characters listed above occurs to some extent within the Allanicytidiidae.

Protocytidium gen. nov.

TYPE SPECIES. *Protocytidium elliottae* sp. nov.

ETYMOLOGY. Greek *proto*, the first and *cytidium*, a small box. Neuter.

DIAGNOSIS. Body subelliptical to pyriform, rarely subrectangular. Convex surface of 12 plates, with 3 in distal row. Medial and lateral orifice plates of plano-concave surface asymmetrical, divided into a 'thecal' portion framing the body orifice and a 'lip' projected distally beyond the orifice. Plate B reduced, not in contact with right lateral orifice plate. Plate A narrow, elongate. Left spine short, slender, almost straight; right spine longer, more robust,

convex, sickle-shaped. Stereom cancellate to honeycomb-like, often replaced by radiating trabeculae near periphery of plates. Styloid trapezoidal, with semicircular blades with radiating trabeculae; proximal blade c.1/2 as large as distal blade.

REMARKS. The phylogenetic position of this new genus is discussed after the specific treatment below but simple distinguishing features are as follows: it differs from all anomalocystitids in the arrangement of the median and lateral orifice plates of the plano-concave surface, shape of the spines and elongate plate A with tiny plate B. *Enoploura* has 5 plates in the distal row on the convex surface, larger C21, different ornament and less expanded styloid. *Occultocystis* has C21 isolated from the proximal body margin, very few plates in the convex surface and C11 and C13 as marginal plates. Most of the advanced genera of the Allanicytidiidae are distinguished by having only C1 and C5 in the distal row on the convex surface, by having straight spines and more elaborate surface ornament.

Protocytidium elliottae sp. nov.
(Figs 1-14)

ETYMOLOGY. For Tracey Elliott of the Palaeontology Department at the Natural History Museum, London.

MATERIAL. Holotype: NMVP100401. Paratypes: NMVP100390-100400, 100402-100403, 100405-100406, 100408-100419, 100421-100436, 100438-100439, 100487-100488 all from NMVPL660.

DIAGNOSIS. As for genus.

DESCRIPTION. EXTERNAL. *Measurements*. Holotype (Fig. 1D): 11mm long, 6mm wide. Largest specimen (Fig. 7C): 14mm long, 7mm wide.

Plano-concave surface (Figs 1A-B,D-E, 2B-D, 4A-B, 6D, 7A,D, 8A, 9B, 10D, 13A). Mostly flat, except for slightly raised lateral margins, with lateral marginal plates divided more or less equally into subhorizontal and vertical parts. Lateral body walls of uniform depth, except for rapid tapering near proximal and distal ends (Fig. 13C-E). PM usually 1.5 times as wide proximally as distally, with straight to concave lateral margins on either side of slight lateral projection just proximal to midlength, with proximal margin strongly embayed for insertion of appendage. PLM with subhorizontal part subtriangular, with convex lateral margin and straight or broadly concave distal margin. ILM as long as PLM,
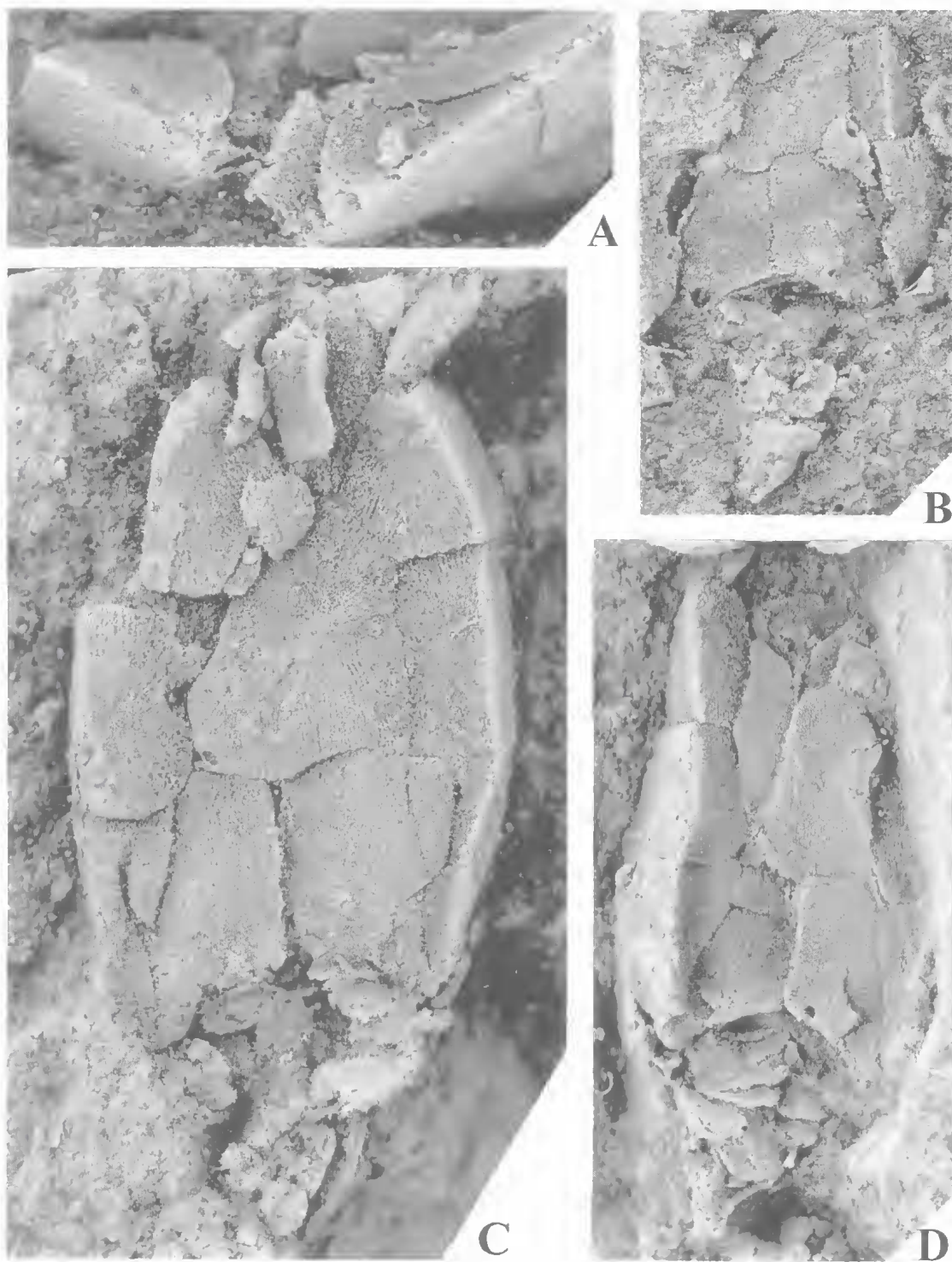
FIG. 2. *Protocytidium elliottae* gen. et sp. nov. A, distal view of distolateral corner of body NMVP100391, ×12. B, partial plano-concave surface of NMVP100397, ×10. C, plano-concave surface incomplete distally, NMVP100410, ×10. D, partial plano-concave surface of NMVP100403, ×7.
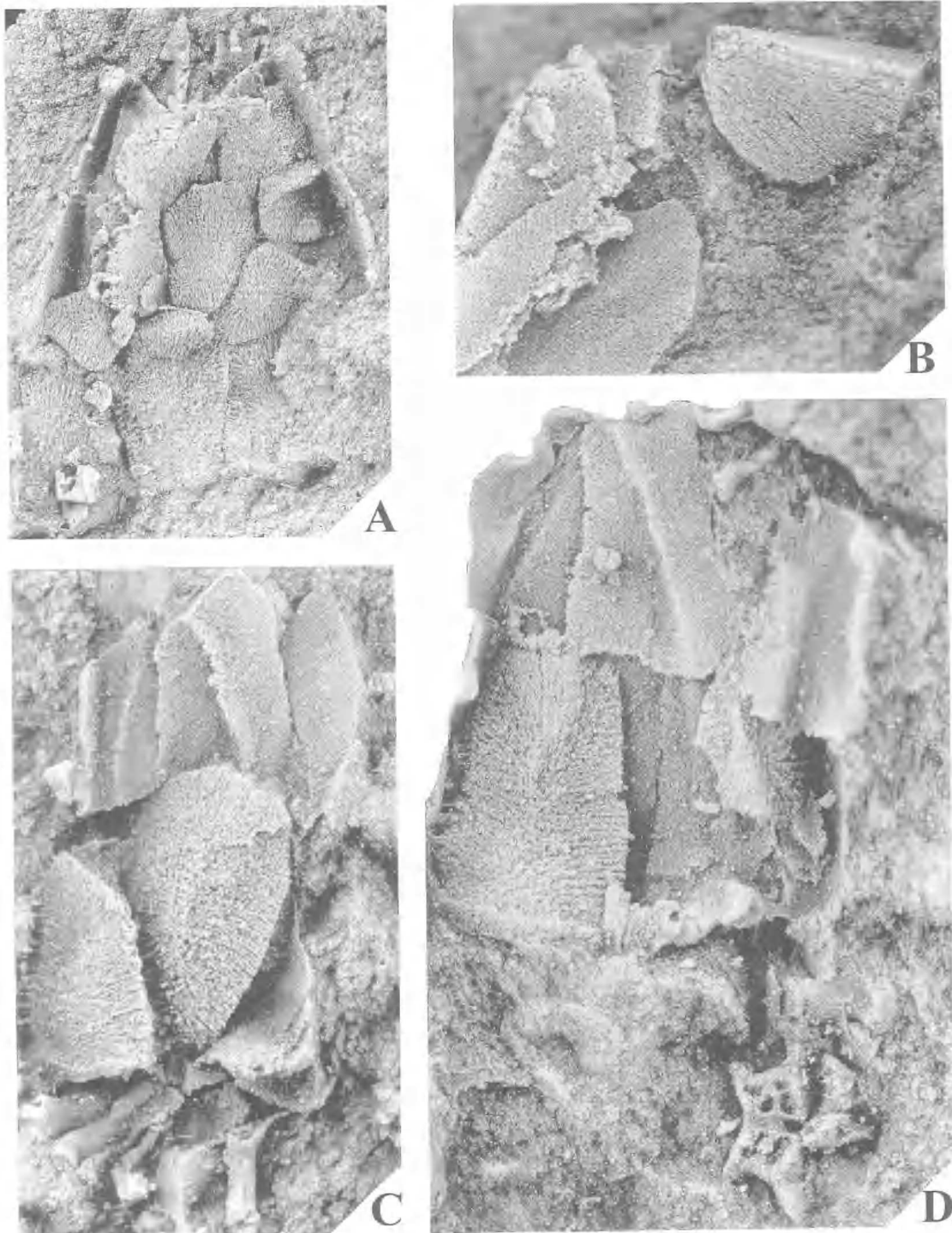
FIG. 3. *Protocytidium elliottae* gen. et sp. nov. A, convex surface of NMVP100488, ×7. B, distolateral corner of mostly disarticulated plano-concave surface of NMVP100391, ×11.5. C, partial proximal convex surface with inside of plano-concave surface in background, NMVP100390, ×6. D, inside of plano-concave surface with C21 still in position and with abapical surface of styloid in lower right, NMVP100417, ×11.5.
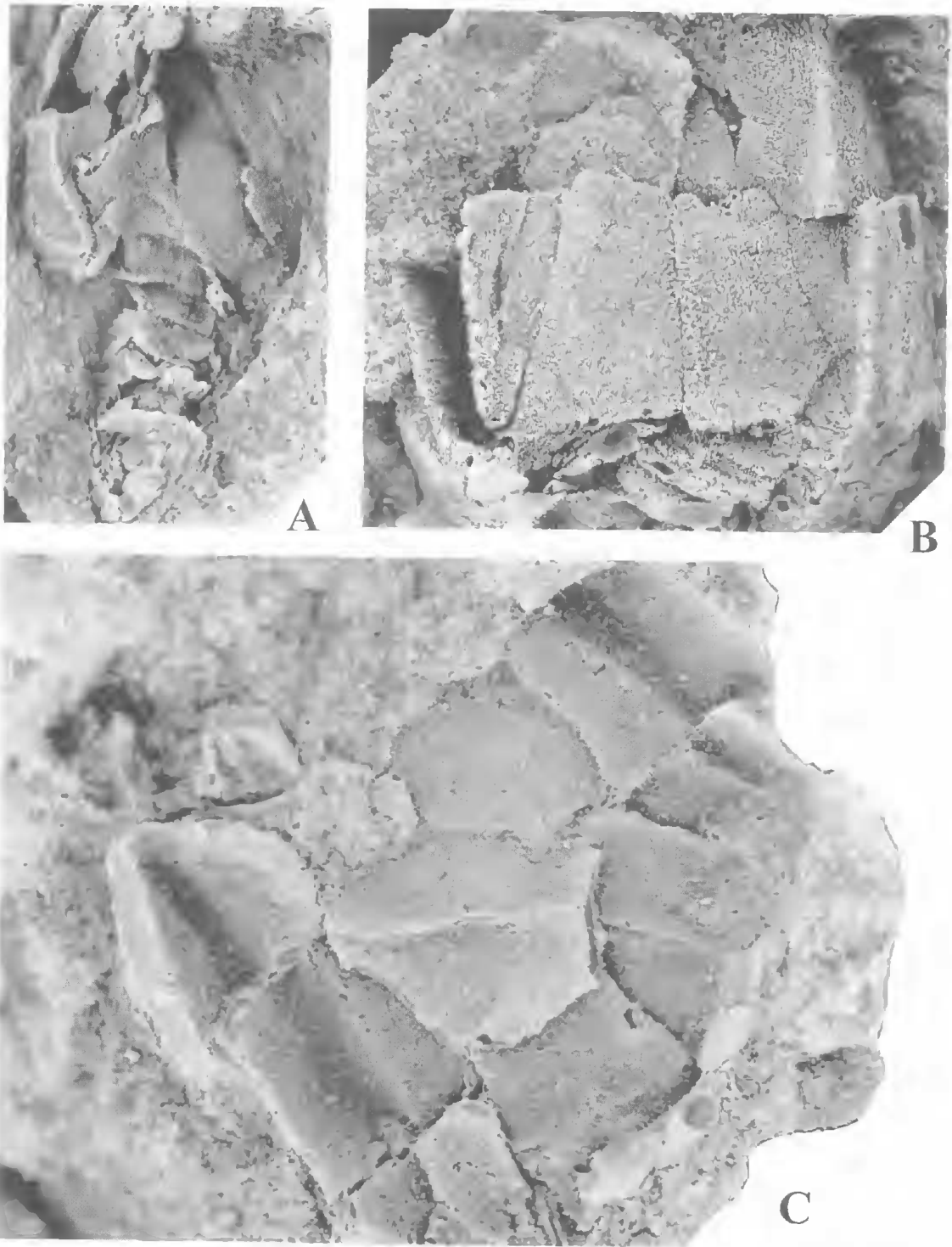
FIG 4. *Protocytidium elliottae* gen. et sp. nov. A, proximal appendage and partial plano-concave surface of NMVP100396, ×8. B, proximal plano-concave surface of NMVP100408, ×10. C, inside of plano-concave surface of NMVP100413, ×12.

subrectangular, with medial margin of right ILM sigmoidal and medial margin of left ILM similarly sigmoidal distal to its junction with the A-C suture and proximally straight, with lateral and distal margins straight. DLM as long as ILM, subrectangular to subtrapezoidal, with shallow distal surface deepening laterally, with subcentral tubercle for spine articulation. LOP and MOP remarkably asymmetrical, at least twice as long as wide, divided into proximal 2/3 articulated with rest of plano-concave surface, and distal 1/3 projecting beyond distal margin of transverse orifice, usually giving rise to irregular process. Irregular gaps between distal parts of adjacent margins of orifice plates. Right LOP generally slightly shorter and narrower than left LOP or MOP.

Plate B subtrapezoidal (based on shape of available plate margins), sutured to left LOP, MOP, A and C. Plate A at least 5 times longer than wide, oblique to longitudinal body axis, sometimes remarkably shortened, with medial margin either gently convex or strongly convex in distal 1/2 and gently concave to straight in proximal 1/2, with pointed proximal wedged between C and left ILM. Plate C widening proximally, in contact with MOP.

Convex surface. All plates except C21 and C3 arranged in pairs (indicated by plate margins and by mirror image arrangement of medial and lateral plates sutured with C20-C22); distal 1/3 of convex surface invariably disrupted and poorly preserved.

C21 with width 40% of length, shield-shaped, with slightly convex longitudinal and transverse profiles; margins very gently convex except straight to weakly concave proximal margin, extreme proximolateral section also with short concave section, producing proximolateral projection. C20 and C22 subtrapezoidal, with maximum width proximally; transverse profile of plates strongly arcuate, especially near their proximo-lateral angle, with thickening immediately distal to proximal margin, with blunt proximo-lateral angles, with medio-distal angles proximal to latero-distal angles. C15 and C19 irregularly pentagonal, with greatest dimension at 45° to body axis, with proximo-medial margins in contact with latero-distal margins of C21, with sigmoidal medio-distal margins. C11 and C13 longer than wide, irregularly hexagonal, sutured along straight median suture. C6 and C9 subtrapezoidal, smallest plates of convex surface, lateral to C11 and C13, respectively.

Distal 1/3 of convex surface poorly preserved in available material, but apparently consisting of 3 large plates in a transverse row (= C1, C3 and C5 based on comparison with *Enoploura* and *Occultocystis*). C5 (Fig. 3A) subrectangular, slightly longer than wide. C3 slightly longer than C5, subpentagonal.

Body stereom and sculpture. External surface of coarse stereomic fabric forming radial pattern on each plate. Terrace-like ridges and riblets absent. Stereom of thick, generally straight, sometimes bifurcating trabeculae often connected by irregularly spaced, short transverse bar-like connections; trabeculae and connections delimit deep pits and become more irregular and randomly branching near plate margins, where the pits are smaller, more numerous and polygonal. Trabeculae of proximal 1/2 of convex surface generally thicker than elsewhere.

C20-C22 (Figs 3A,C-D, 5C) with trabeculae almost parallel to each other, rarely bifurcating, gently arcuate or straight near lateral and medial margins of C20 and C22, becoming confluent near centre of proximal 1/2 of external surface of both plates, where they become slightly thicker and irregularly sinuous, with trabeculae on distal 1/2 thinner, subparallel to body axis, converging to centre of plates proximally. C21 with broadly arcuate trabeculae separated by granular fabric on proximal 2/3, with distal trabeculae straight, bifurcating, in fan-like arrangement. Remaining body plates with gradual changes in stereom structure from centre to periphery (Figs 1A-B,D-E, 2C-D, 4B, 7A-B,D, 8A-C, 9B, 10D); centre compact or honeycomb-like, with short, anastomosing trabeculae; more peripheral stereom of elongate trabeculae with transverse connections; surface with cancellate or honeycomb-like fabric proportional to plate size. Orifice plates with shallow pits and poorly defined, flat-topped trabeculae or coarse and without obvious surface pattern. Proximo-distally elongate trabeculae near proximal and distal margins of PLM, ILM and DLM (Fig. 1F-G). External surface of A and B (Fig. 1D) with large, widely spaced polygonal pits delimited by thin trabeculae. PM with honeycomb fabric, with radiating peripheral trabeculae, especially along distal margins.

Spines. Left spine straight or gently convex externally, round in cross-section, with clavate proximal end, with hemispherical articular surface, tapering distally, with blunt terminus. Right spine slightly longer and twice as wide as left spine, sickle-shaped, flattened except for
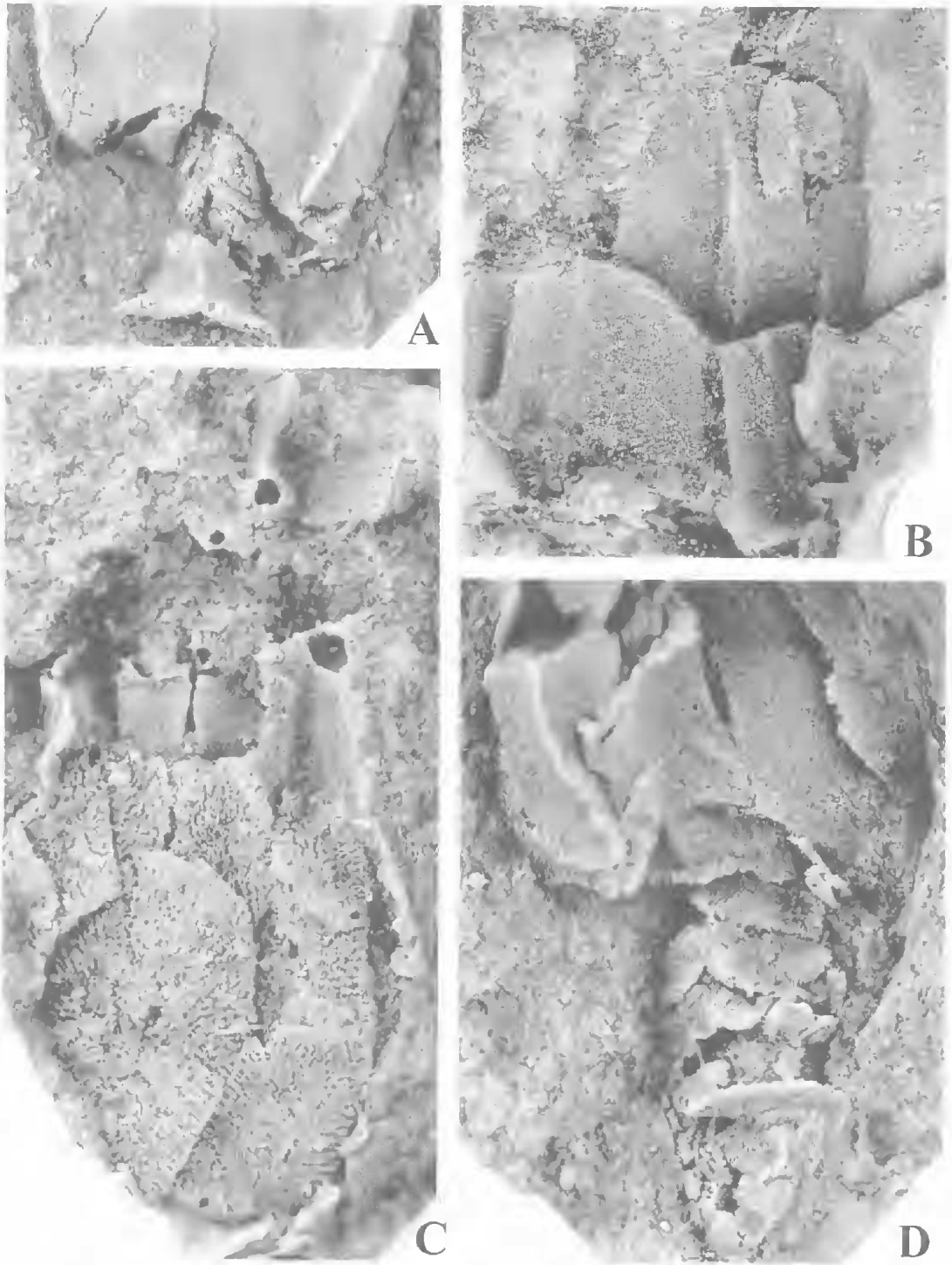
FIG. 5. *Protocytidium elliottae* gen. et sp. nov. A. styloid and proximal part of plano-concave surface of NMVP100424, ×8. B, inside of plano-concave surface of NMVP100423, ×12. C. partial convex suface with distal row removed to show inside of orifice plates of NMVP100398, ×12. D. proximal appendage and proximal plano-concave surface of NMVP100396, ×12.
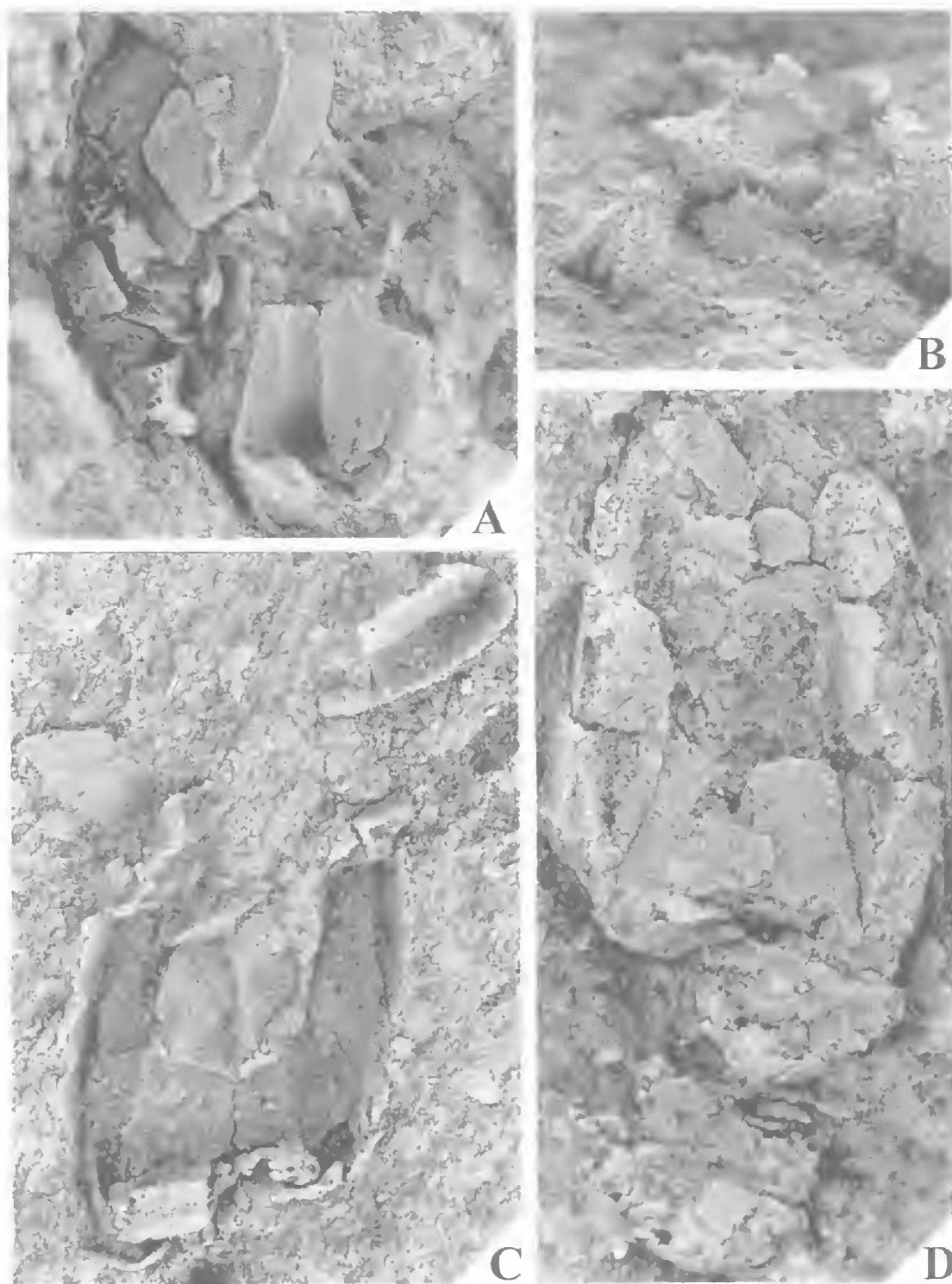
FIG. 6. *Protocytidium elliottae* gen et sp. nov. A. inside of plano-concave surface of disarticulated NMVP100398, ×8. B, styloid of NMVP100430, ×12. C, inside of plano-concave surface of NMVP100487, ×7. D, plano-concave surface of NMVP100394, ×9
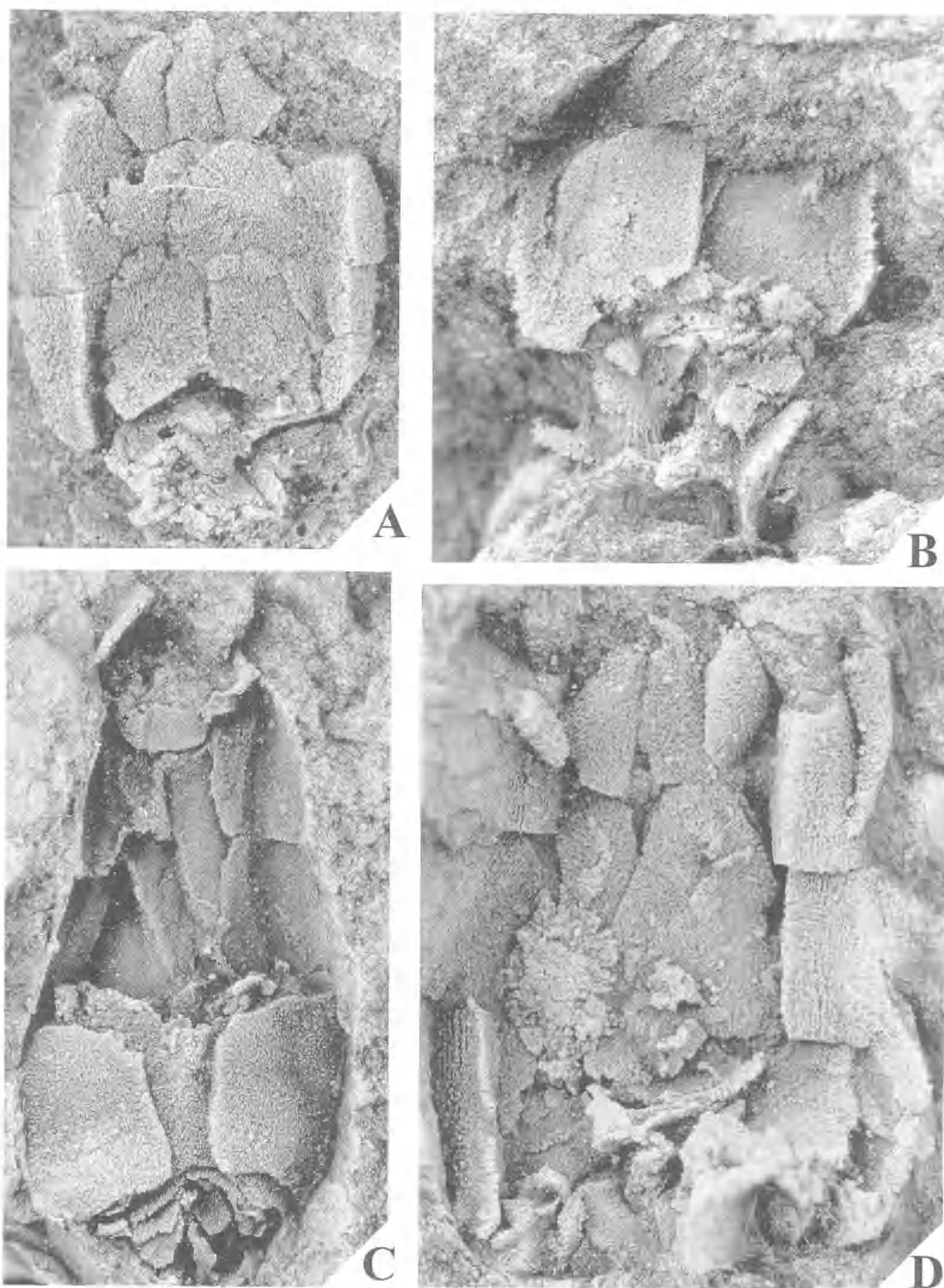
FIG. 7. *Protocytidium elliottae* gen. et sp. nov. A, plano-concave surface showing orifice plates of NMVP100402, ×10. B, proximal parts of plano-concave surface and appendage of NMVP100414, ×10. C, interior of plano-concave surface but with proximal part concealed by C20-C22 still in place of convex surface, NMVP100403, ×7. D, plano-concave surface with orifice plates intact, NMVP100395, ×9.

being conical distally, with sharp lateral and blunt medial margins, tapering distally to point, with subconical articular projection with 2 facets separated from short subcylindrical region by poorly pronounced ridge, with stereom of minute, irregular, shallow pits separated by coarsely granular to compact texture.

INTERNAL. *Plano-concave surface.* Internal surface of orifice plates divided into 2 unequal parts and different depths by transverse, distally concave thickening (Figs 7C, 8D, 9D, 11D, 12D). Internal surface of left latero-distal angle of body occupied by subtriangular area straddling suture between left DLM and left LOP and medial to tubercle for spine insertion on left DLM. Proximo-lateral 1/2 of subtriangular area slightly deeper and more raised than medio-distal 1/2 and delimited laterally and proximally by 2 ridges, continuing distally on internal surface of left LOP where the proximal, thicker ridge (pr in Fig. 12A) almost parallels the body axis, with the thinner ridge (lar in Fig. 12A) widening rapidly in its distal 1/2 before giving rise to thickened lateral margin of internal surface of left LOP, with central part of subtriangular area occupied by pit (p in Fig. 12A). Proximal and lateral ridges merging and continuing as a low sinuous ridge (lr in Fig. 12A) coinciding with junction between subhorizontal and vertical parts of plate. Distal 1/4 of low ridge with triangular lateral process (lp in Fig. 12A) partially delimiting shallow subelliptical area (sa in Fig. 12A). Low ridge of right side apparently fading gradually distally near medio-distal angle of internal surface of right ILM, immediately lateral to point where the oblique septum (see below) straddles the suture between C and right DLM and abruptly changes direction. Oblique septum (se in Fig. 12C) with asymmetrical transverse section running from distal right angle to proximal left angle of inside of plano-concave surface (Figs 3C-D, 4C, 5B, 6A,C, 7C, 8D, 9A,C-D, 10C, 11A, 12C), with proximal 1/3 straight or gently convex to left, with proximal end merging into left scutula (sc in Fig. 12C). Left scutula transversely elongate (Figs 3D, 6A,C, 9C). Straight, transverse ridge (tr in Fig. 12C) (sensu Ruta & Jell, 1999a) delimited proximally by transverse furrow (tf in Fig. 12C). Second ridge, probably homologous with the proximal ridge of Ruta & Jell (1999a) (dr in Fig. 12C), running from left scutula to lateral margin of left PM, bending rapidly latero-distally and continuing on internal surface of left PLM as the most proximal part of the low ridge described above (lr in Fig. 12C). Apophyseal horns (ah in

Fig. 12C) gently convex in transverse section, with straight proximal margin and gently convex distal margin in plan view, with medial ends separated by small gap (Fig. 9C). Septum (sc) on plate C divided into a straight proximal 1/2 and narrower, gently convex to the right or sinuous distal half. Distal 1/3 of septum gently convex to the right, proximo-distal on inside of right DLM. Distally, septum has T-shaped birfucation near latero-distal angle of right DLM.

Convex surface. Inside of convex surface poorly preserved (Figs 1A, 11E). Co-operculum cup-like, just distal to midpoint of proximal margin of C20 and C22, with irregular rim, thicker in its distal 1/2 than in its proximal 1/2, with narrow slit at proximo-medial angle. Low oblique crest running medio-distally from medio-distal angle of co-opercular rim (Fig. 1A). C21 with weak struts radiating from point proximal to midlength (Fig. 1A) and reaching its proximal margin, with proximo-distally elongate, low, poorly defined ridge centrally (Fig. 11E), gradually disappearing distally.

Stereom. Inside of plano-concave surface with minute pits or, more frequently, honeycomb-like. Plate peripheries usually with minute pits sometimes very shallow and surrounded by poorly defined trabeculae. Proximal part of MOP and LOP compact or coarsely fibrillar, rarely with shallow, subelliptical pits and small lumps; distal part of orifice plates coarsely granular or with radiating and often bifurcating trabeculae separated by deep furrows (Figs 7C, 9D, 11D). Stereom of inside of convex surface cancellate to coarsely granular, of low anastomosing trabeculae separated by shallow elongate pits (Fig. 11E).

APPENDAGE. Proximal part of 6-7 tetramerous overlapping rings; ring plates of uniform width, in sutured contact mid-longitudinally and laterally. Ring plates on plano-concave side of body subrectangular, convex in transverse section, with straight proximal margins, with distal margins gently convex or sinuous and slightly thickened. Ring plates on convex side narrower, with straight proximal and distal margins. Styloid 3 times as wide as long, maximum width at distal blade, with low median keel. Proximal blade with semicircular, blunt free margin and flat to gently convex distal surface. Distal blade proximally recumbent, with semicircular sharp free margin, with flat surfaces, with proximal surface sometimes divided into 2 slightly convex halves (Figs 2B, 7B). Abapical surface of styloid (Figs 3D, 12E) gently concave
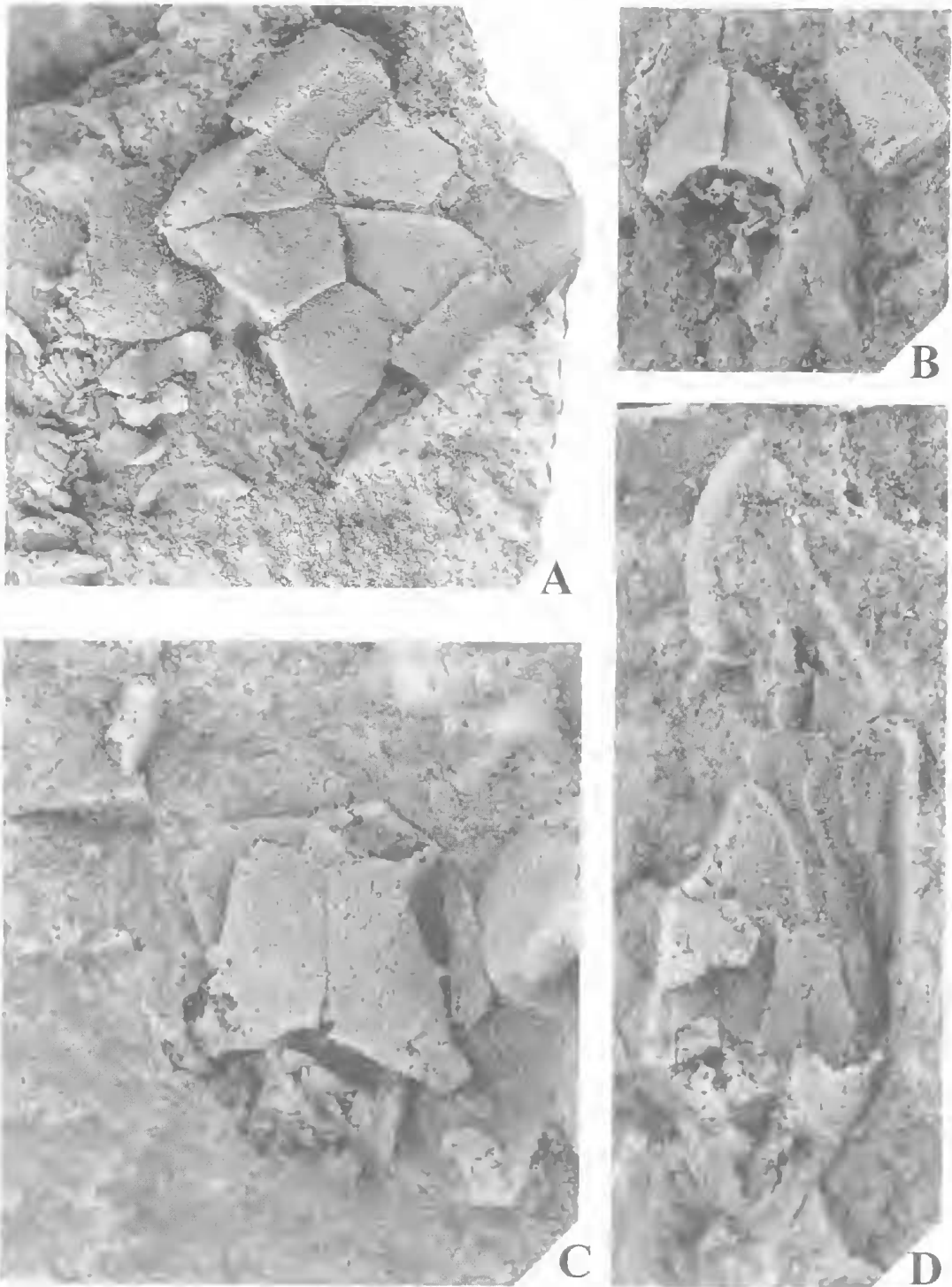
FIG. 8. *Protocytidium elliottae* gen. et sp. nov. A, proximal plano-concave surface and appendage plates of NMVP100413, ×7. B, proximal plates of plano-concave surface and parts of appendage of NMVP100391, ×6. C, PM plates over inside of convex surface plates of NMVP100419, ×12. D, inside of plano-concave surface of NMVP100401, ×12.
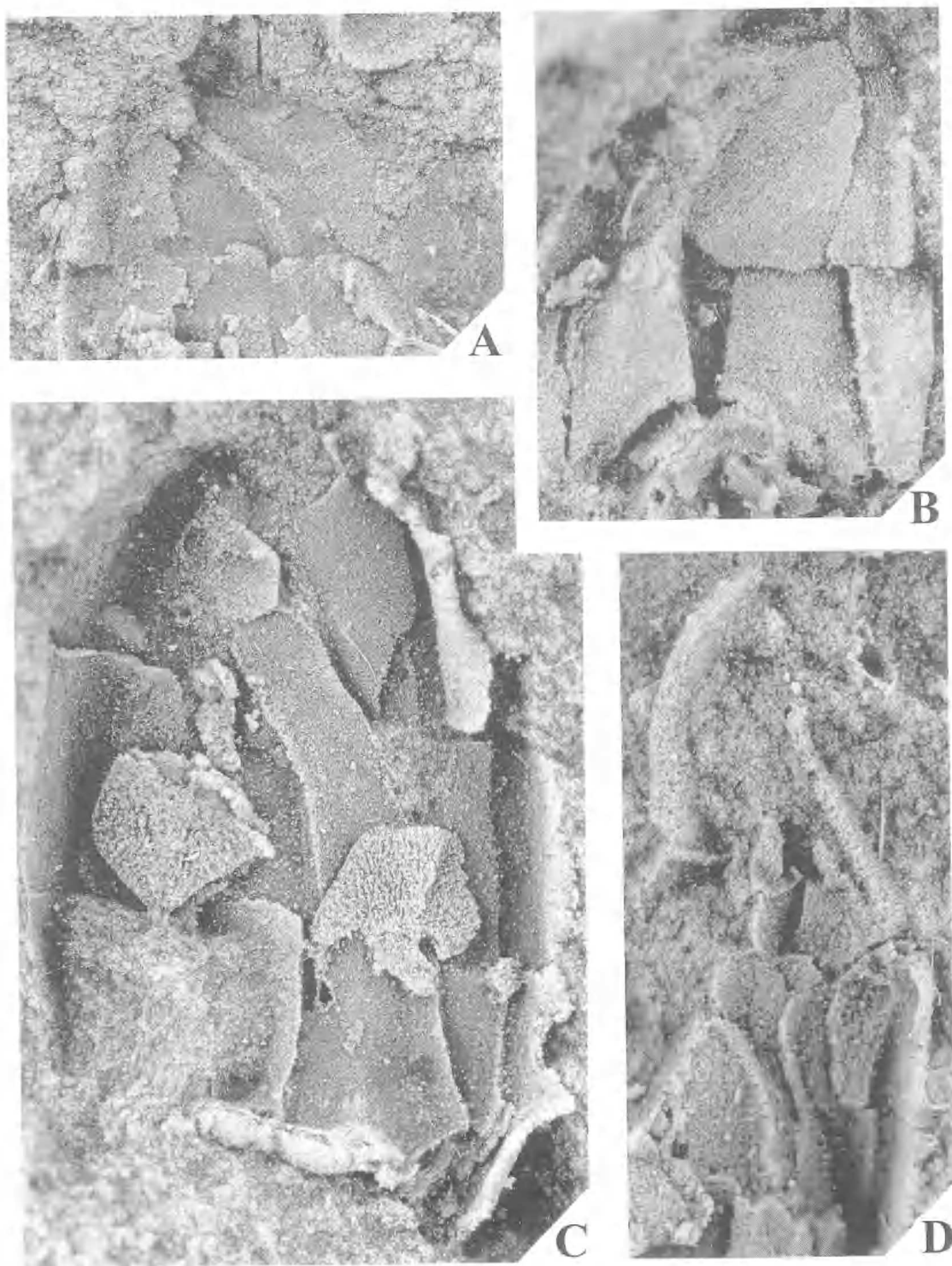
FIG. 9. *Protocytidium elliottae* gen. et sp. nov. A, inside of plano-concave surface and orifice plates of NMVP100392, ×7. B, partial plano-concave surface of NMVP100409, ×12. C, inside of plano-concave surface of NMVP100418, ×12. D, detail of distal part of Fig. 8D, NMVP100401, ×15.
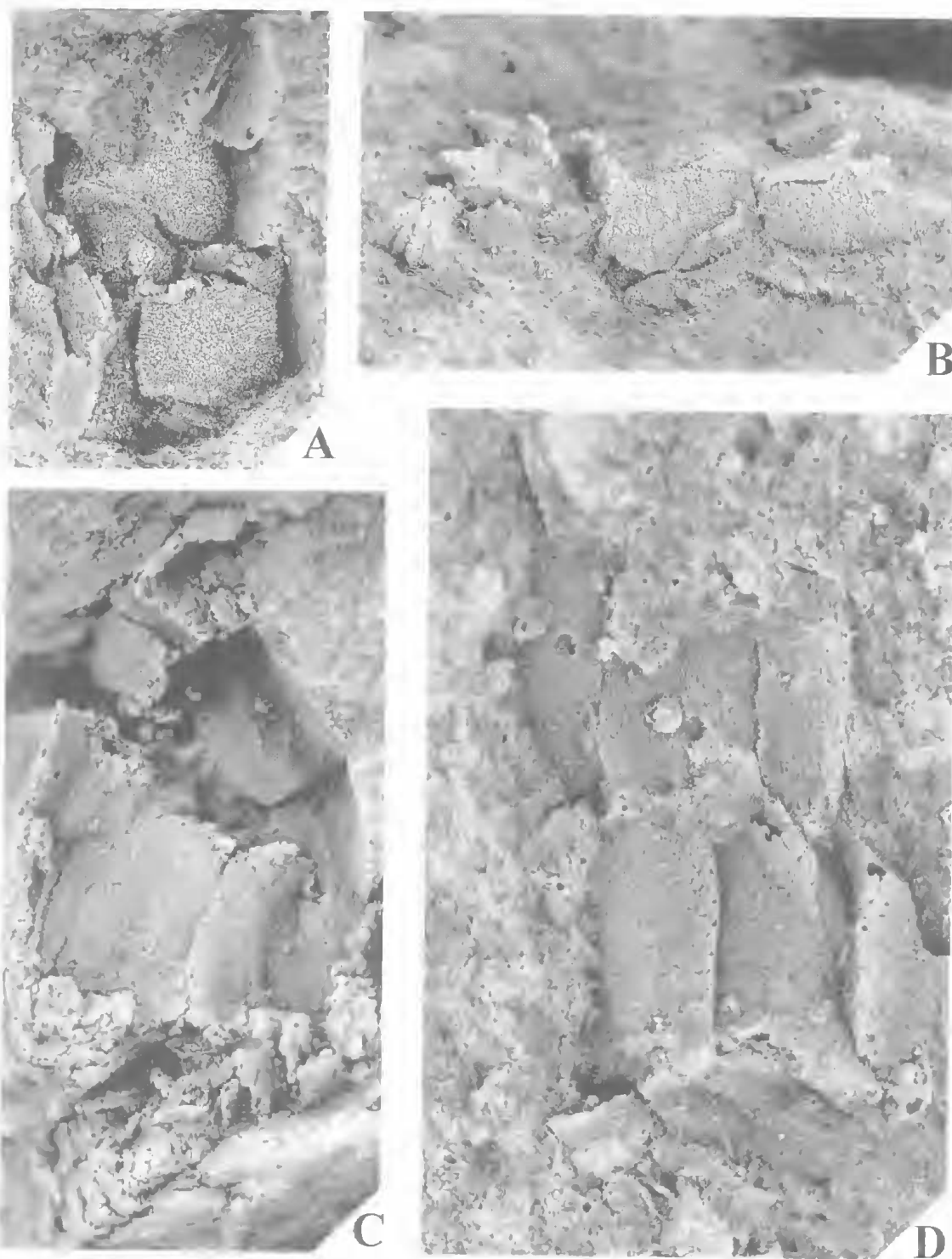
MEMOIRS OF THE QUEENSLAND MUSEUM

FIG. 10. *Protocytidium elliottae* gen. et sp. nov. A, partial convex surface. NMVP100435, ×7. B, lateral view of proximal appendage and plano-concave surface of NMVP100430, ×8. C, inside of plano-concave surface of NMVP100399, ×12. D, partial convex surface of NMVP100416, ×12.

in transverse section, with slightly raised proximal and distal margins, with straight central longitudinal furrow (sf in Fig. 12E) along proximal 2/3 of styloid, of uniform depth and width, shallowing to rounded proximal termination and distally in subelliptical pit (sp in Fig. 12E), with proximal margin slightly concave medially. Articular surface (Fig. 12E) with 4 irregular pits laterally on left and right.

Distal part. Largest observed number of ossicles 11 (Fig. 1D), articulated with paired plates. Ossicles only slightly higher than wide, triangular in cross-section (Fig. 10C), diminishing in size distally; lateral surfaces flat or gently convex in abapical 1/2, slightly depressed in apical 1/2; apical margin blunt, sloping distally, with blunt bulbous apex. Apex developed mainly on 3 or 4 most proximal ossicles, decreasing rapidly distally, absent on distal ossicles. Articular margins of ossicles along zig-zag line, divided into smaller, distal portion in contact with plate of next distal segment and larger, proximal part sutured with plate of corresponding segment. Plates subrectangular, partly overlapping each other proximo-distally. Articular margin of plates thicker proximally, gently tapering distally.

Stereom. Appendage externally with shallow irregular pits. Tetramerous rings and free margins of styloid blades sometimes coarsely granular. Radiating trabeculae on both styloid blades.

REMARKS. Material is often considerably disrupted and partly deformed. Very few specimens approach completeness, and the distal part of the convex surface is invariably damaged or missing. In some cases, the body plates are disarticulated but lie close to each other so that their mutual spatial relationships are almost unchanged. Preservation of the plano-concave surface is generally better than that of the convex surface, but the precise arrangement of the orifice plates can be deduced only by combining information from different individuals. In some specimens, both spines are visible and in the holotype, these are found in close proximity to the body, although only the left spine is preserved articulated with the toroidal projection on the distal surface of left DLM. The appendage is always incompletely preserved, although isolated ring plates of the proximal part, the abapical surface of the styloid and external ossicle morphology can be reconstructed.

Despite tectonic deformation, it is possible to distinguish 2 morphological variants.

Homologous plates in individuals belonging to these variants show slightly different length/width ratios (e.g. PLM, 1LM and DLM) and, sometimes, remarkably different shapes (e.g. A and C). The possibility that the 2 variants represent the effects of compression of the body along different directions cannot be entirely ruled out. Intraspecific and ontogenetic variation or sexual dimorphism could also be responsible. Similar problems were discussed by Ruta & Bartels (1998) in their analysis of tectonic deformation in *Rhenocystis latipedunculata* Dehm, 1932. Unlike *Rhenocystis*, specimens of *P. elliottae* have not been found in proximity to one another on the same slab surface and, therefore, retrodeformation techniques could not be applied to the Australian taxon. The first variant is more frequently represented with elongate, subelliptical to pyriform body outline and usually has markedly elongate plates A and C. In the second, rarer variant the body is only slightly longer than wide, subrectangular; both marginal and central plates of plano-concave surface are shorter; in particular, A and C are wider than long, subrhomboidal in outline and of equal width. The 2 variants do not seem to be related to body size, although some specimens belonging to the first category are among the largest known.

ORIGIN AND EVOLUTION OF THE ALLANICYTIDIIDAE

Established by Caster & Gill (1967) to accommodate Early Devonian *Allanicytidium flemingi* from the Reefton Group of New Zealand, the Allanicytidiidae has expanded to now include 7 Southern Hemisphere anomalocystitids (*Allanicytidium, Notocarpos, Tasmanicytidium* and *Protocytidium* from Australia, *Placocystella* from South Africa and *Occultocystis* and *Australocystis* from South America). Philip (1981) recognised the almost identical plating pattern in *Allanicytidium* and *Notocarpos garratti* (Ludlow), although he did not note the lateral orifice plates in the latter taxon and misinterpreted the arrangement of C20 and C22 (Caster, 1983). Caster (1983) provided a diagnosis and revision of the allanicytidiids with his description of *Tasmanicytidium burretti* (Llandovery). Haude (1995) modified the diagnosis to include *Occultocystis koeneni* (Early Devonian). Prior to discovery of *Protocytidium, Occultocystis* provided the only link between Late Ordovician mitrate faunas from Laurentia and mid-Palaeozoic mitrates from Gondwana.
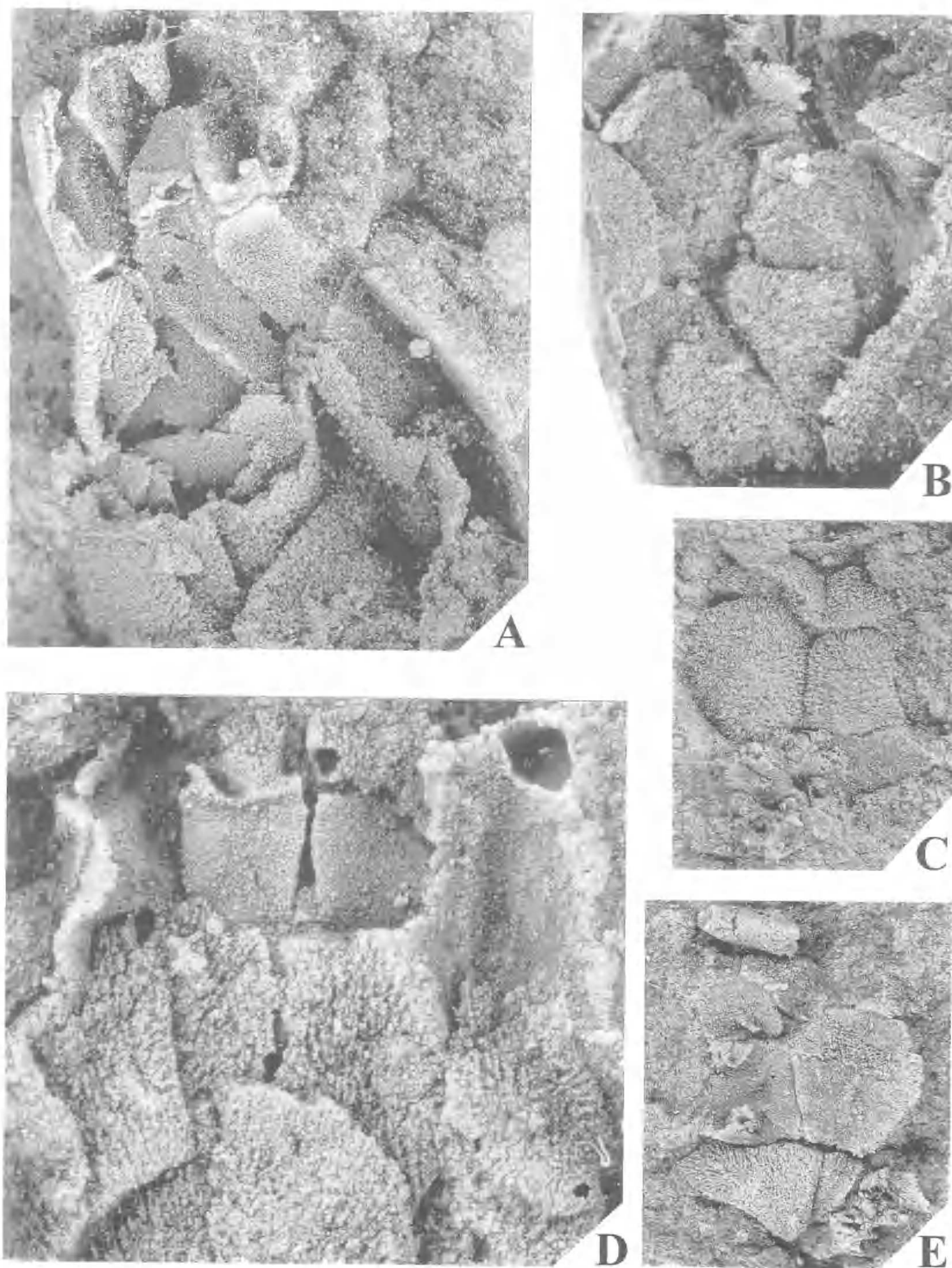
FIG. 11. *Protocytidium elliottae* gen. et sp. nov. Inside of plano-concave surface, convex surface, orifice plates and stereom. A, inside of plano-concave surface of NMVP100421, ×12. B, partial convex surface of NMVP100400, ×12. C, E, partial convex surface of NMVP100428, ×7. D, detail of distal part of Fig. 5C showing inside of orifice plates of NMVP100398, ×20.
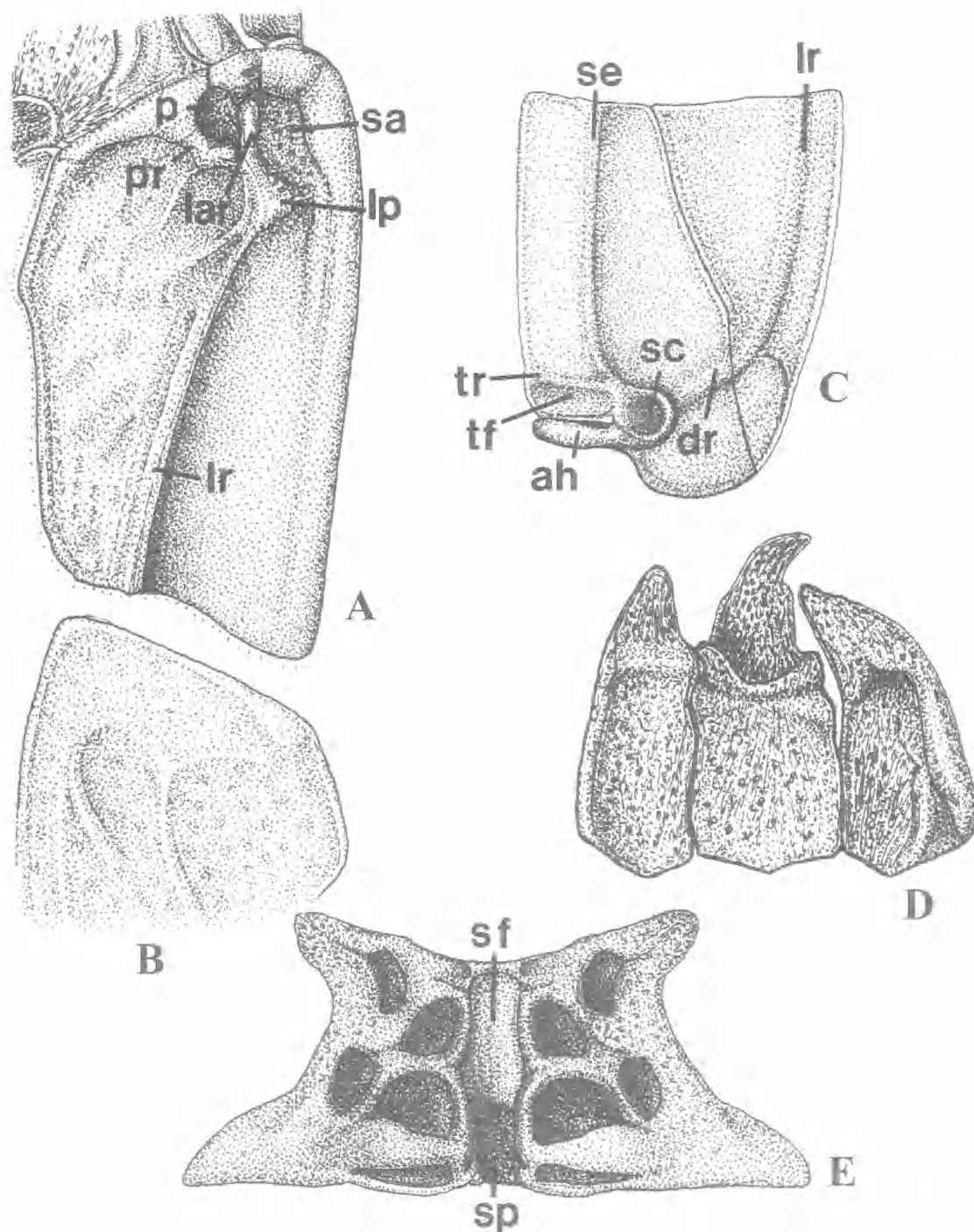
FIG. 12. *Protocytidium elliottae* gen. et sp. nov. Reconstruction of internal features of body. A, left DLM and left LOP, based on NMVP100401. B, right DLM based on NMVP100418. C, left PLM and left PM, based on NMVP100393. D, inside of MOP and LOP, reconstructed from NMVP100398, 100401, 100403 and 100488. E, abapical surface of styloid, based on NMVP100417. Abbreviations as in text. Drawings not to scale.
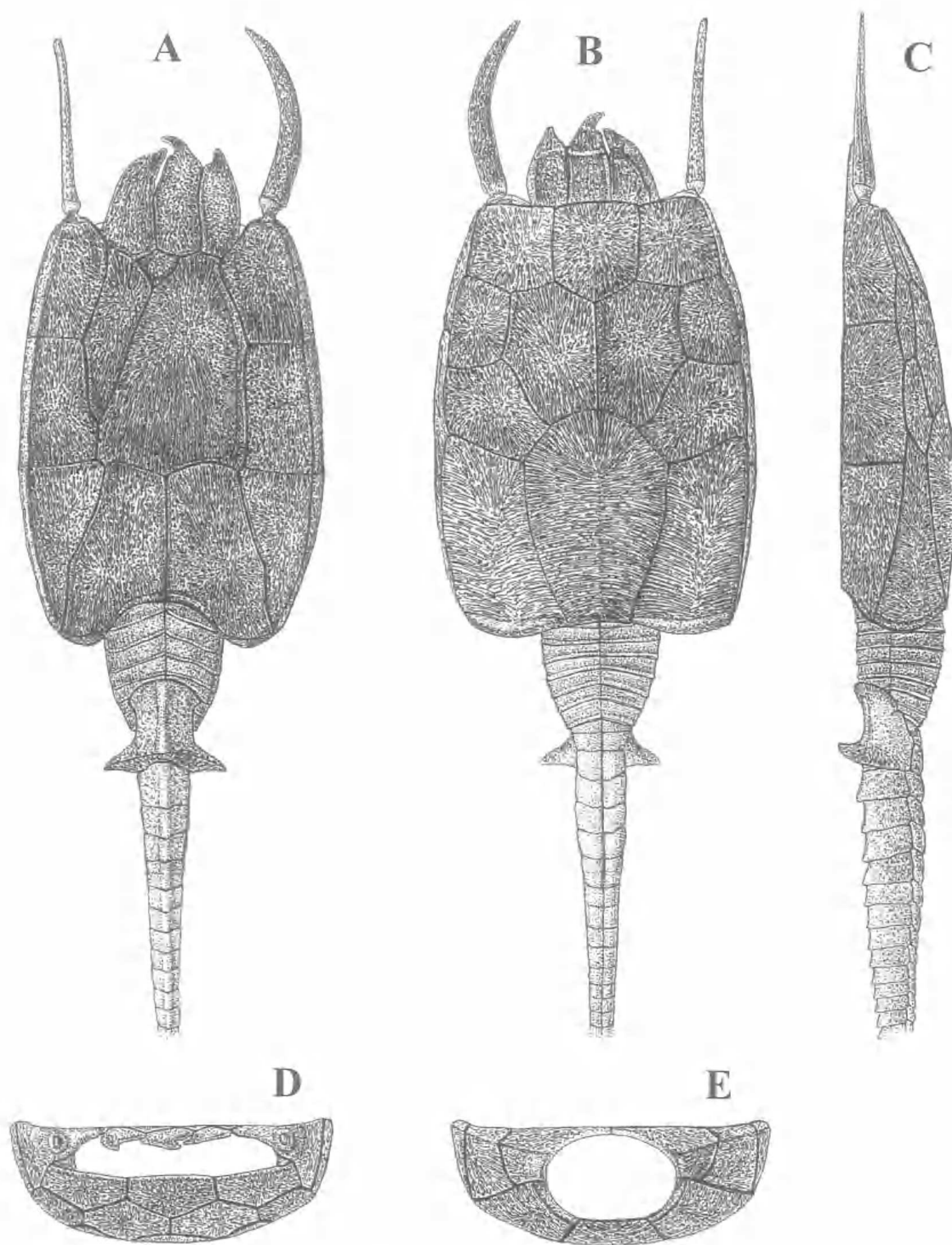
FIG. 13. Reconstruction of *Protocytidium elliottae* gen. et sp. nov. A, plano-concave surface. B, convex surface. C, right lateral view. D, proximal view (spines omitted). E, distal view (appendage omitted).

Character analysis of the allanicytidiids and relatives was undertaken by Ruta & Theron (1997). *Enoploura* is the sister-group to monophyletic Allanicytidiidae (Ruta in press). Ruta & Theron (1997) assigned *Placocystella africana* (Reed, 1925) and *Australocystis langei* Caster, 1956 (Early Devonian) to the Allanicytidiidae and recognised that the plano-concave surface of *Tasmanicytidium* is similar to that of more derived allanicytidiids (Caster, 1983; Ruta, in press).

Mongolocarpos minzhini Rozhnov, 1990 (Ludlow; Mongolia) is removed from the Allanicytidiidae despite the proximo-distal elongation of plate A. It is here considered a close relative of *Placocystites, Rhenocystis* and *Victoriacystis* following Ruta (in press).

ENOPLOURA AND THE ORIGIN OF THE ALLANICYTIDIIDS.

Enoploura popei Caster, 1952 (Fig. 14A) has been described in great detail (Caster, 1952; Parsley, 1991). Its distalmost transverse row of plates on the convex surface has 5 elements as in *Barrandeocarpus norvegicus* Craske & Jefferies, 1989 and the anomalocystitids *Anomalocystites cornutus* Hall, 1858, *Bokkeveldia oosthuizeni* Ruta & Theron, 1997, *Mongolocarpos minzhini* Rozhnov, 1990, *Placocystites forbesianus* de Koninck, 1869, *Rhenocystis latipedunculata* Dehm, 1932 and *Victoriacystis wilkinsi* Gill & Caster, 1960. The lateral plates of the distalmost transverse row in *Enoploura* overlap the admedian plates as well as the marginal plates just proximal to them (Parsley, 1991). These marginal plates and the 2 large central plates lying medial to them may correspond to C6-C9 in *Bokkeveldia*, in which the admedian plates of row II, C7 and C8, are relatively large in comparison with other plates of the convex surface, as well as in other anomalocystitids. As an alternative hypothesis, the marginal plates sutured with C20 and C22 and the two large central plates of the convex surface of *Enoploura* may be homologous with the lateral (C15 and C19) and admedian (C16 and C18) plates of row IV in *Bokkeveldia*.

Enoploura and *Ateleocystites guttenbergensis* Kolata & Jollie, 1982 are similar in configuration of rows II and III in the latter resembling that of the 2 distalmost rows of *Enoploura*. Thus, *Enoploura* differs from *Ateleocystites* in possessing a shortened convex side (Parsley, 1991) in which the distal, 5- plated row would correspond to row II of *Ateleocystites*; the row

proximal to it would be homologous to row III of *Ateleocystites* and the 2 marginal elements in contact with C20 and C21 on the right side and with C21 and C22 on the left side would correspond to the lateral elements of row IV (C15 and C19) in *Atcleocystites*. Furthermore, the proximo-distal imbrication pattern of the 2 large central plates of *Enoploura* is similar to that of the admedian elements of row III (C11 and C13) in *Ateleocystites*.

According to Parsley (1991), the body of *Enoploura* is progenetically shortened in comparison with that of other mitrates. This is an intriguing hypothesis, but it needs to be corroborated by additional fossil evidence. A derivation of *Enoploura* from taxa with a polyplated convex surface is likely, but not certain. Despite its specialised features (e.g. morphology of the styloid; plate arrangement of the convex surface), *Enoploura* retains a primitive skeletal configuration on the plano-concave surface, as indicated by plate B. Such a configuration suggests that this genus probably evolved from an ancestor resembling such Laurentian genera as *Ateleocystites* (Ruta, in press).

PROTOCYTIDIUM: BASAL ALLANICYTIDIID. Skeletal configuration of *Protocytidium elliottae* (Fig. 14B) invites comparisons with *Enoploura* and with such basal allanicytidiids as *Occultocystis*. Affinities of *Protocytidium* with the allanicytidiids are suggested by the central plates of the plano-concave surface, especially the proximo-distally elongate plate A, and by the longitudinal styloid keel, a semicircular, proximal styloid blade and a proximally recumbent distal blade. The distal 2/3 of C21 is similar in shape and proportions to its homologue in *Tasmanicytidium*.

However, although plate A is more elongate and narrower than in *Notocarpos* and is shaped like its homologue in such allanicytidiids as *Placocystella*, it does not contact left PLM as in all allanicytidiids more derived than *Notocarpos* (Caster, 1956, 1983; Caster & Gill, 1967; Ruta & Theron, 1997; Ruta & Jell, 1999c; Ruta, in press). Although MOP is longer than LOP, it is not as expanded transversely as in *Notocarpos, Tasmanicytidium, Placocystella, Allanicytidium* and *Australocystis*. Furthermore, both LOP plates are wider proximally than distally and not wedged obliquely between MOP and DLM (MOP and LOP not known in detail in *Occultocystis*).
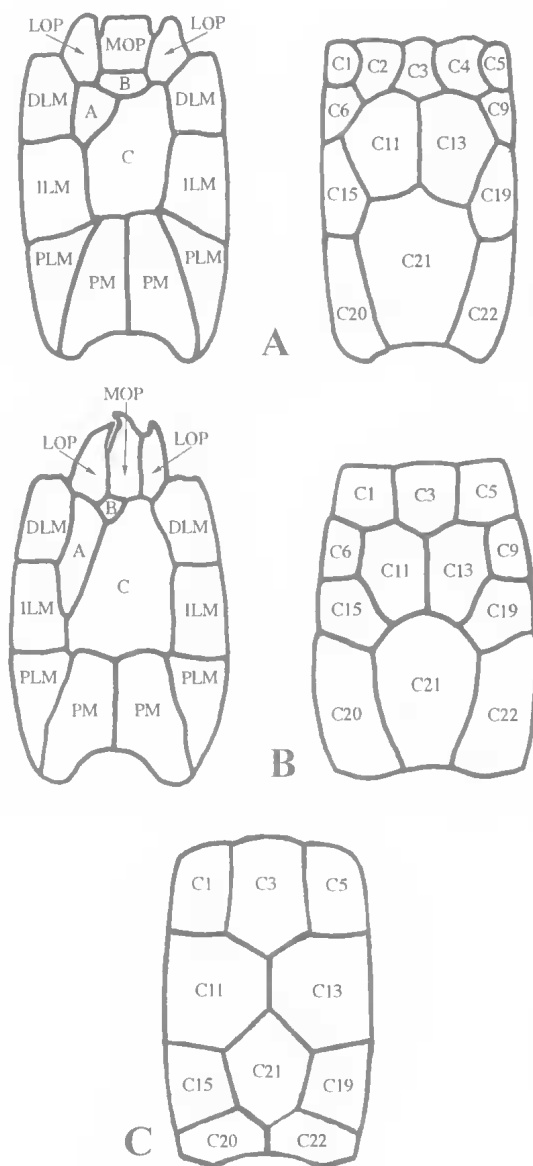
FIG. 14. Plano-concave (left) and convex (right) surfaces of A, *Enoploura popei* (redrawn and modified from Parsley, 1991). B, the basal allanicytidiid *Protocytidium elliottae*. C, convex surface of *Occultocystis koeneni* (redrawn and modified from Haude, 1995). Drawings not to scale.

Except for the occurrence of 3 (as in *Occultocystis*) rather than 5 distal plates, skeletal configuration of the convex surface of *Protocytidium* differs from that of *Enoploura* mainly in the relative size and proportion of various plates. The 3 distalmost plates of the

convex surface (especially C3) are larger in *Protocytidium* than in *Euoploura* but smaller than in *Occultocystis*. Both in *Enoploura* and in *Protocytidium* LOP and MOP project distal to the body orifice and are divided into proximal and distal parts ('thecal' and 'lip' of Parsley, 1991). Gaps are present distally between MOP and LOP but they are smaller and more irregular than in *Euoploura*. The transverse thickening on the internal surface of LOP and MOP is another similarity between *Protocytidium* and *Enoploura*. More striking resemblances are on the internal side of the plano-concave surface, especially in the asymmetrical development of internal ridges near the latero- distal angles of the left and right DLM.

Plate B, generally regarded as a primitive character for the anomalocystitids (Craske & Jefferies, 1989; Ruta & Theron, 1997; Ruta, in press), is much smaller in *Protocytidium* than in *Enoploura* and other mitrates and appears to be displaced slightly to the left of the longitudinal body axis. Furthermore, B does not contact right LOP and is strongly asymmetrical in outline. C6, C9, C15 and C19 of *Enoploura* differ from their homologues in *Protocytidium* in being much longer than wide. Relative size and proportions of C11, C13 and C21 are similar in both taxa.

The coarsely pitted to labyrinthine stereom in *Enoploura popei* (Caster, 1952; Parsley, 1991) is only vaguely reminiscent of the external skeletal texture of *Protocytidium*. The latter appears to be less coarse, presumably as a result of the much smaller body size of *Protocytidium*, and more variable both on the surface of single body plates and on different plates. Resemblances between the body stereom of *Enoploura* and that of *Protocytidium* nevertheless occur in the vermicular to ridge-like pattern of C20 and C22 and the lateral body walls.

TRANSITIONAL *OCCULTOCYSTIS*. In *Occultocystis* (Fig. 14C), C21 is not as large as in other allanicytidiids and is not interposed between C20 and C22. On both right and left of its convex surface, a plate may occur which is perhaps incompletely fused with C20 and C22 respectively (Haude, 1995). The distal margin of the convex surface consists of 3 plates, of which the median one is narrow and elongate with concave lateral margins as in *Enoploura*. It is likely that the marginal plates sutured along the midline of the convex surface of *Occultocystis* are homologous with the 2 large central elements of *Enoploura*.
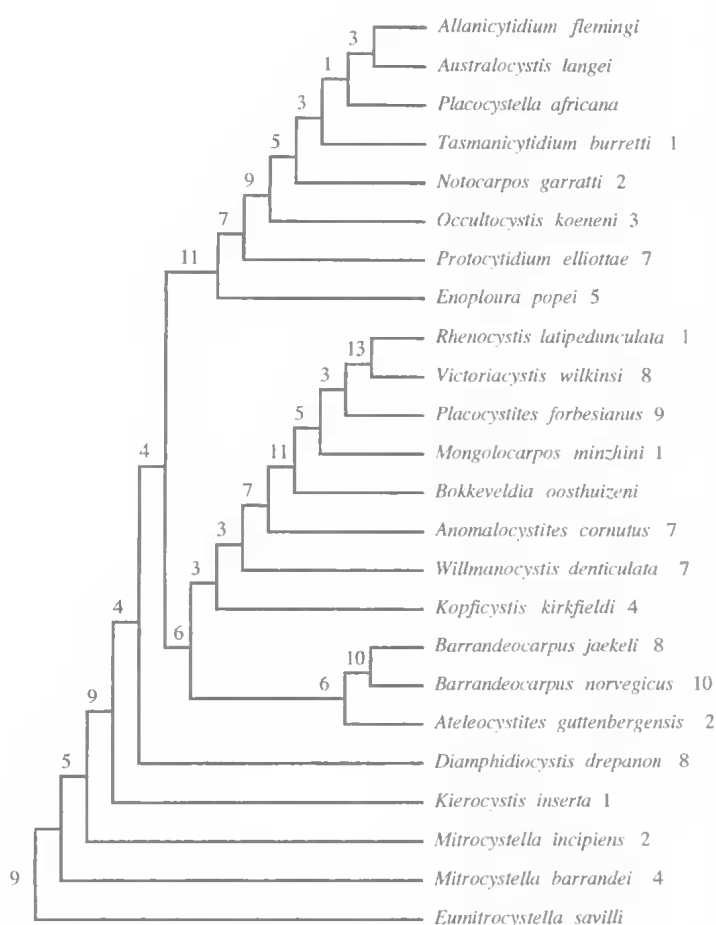
FIG. 15. Most parsimonius tree resulting from cladistic analysis. Numbers indicate branch lengths.

here to establish the phylogenetic position of *Protocytidium elliottae*. Morphological characters are those discussed by Ruta (in press) with coding for *Kierocystis inserta* Parsley, 1991 accounting for the reconstruction of the proximal 1/3 of the convex surface proposed by Parsley (1991; pers. comm., 1997). Some characters of the spines are entered as polymorphic for *Protocytidium*. The matrix includes 24 taxa and 106 binary characters and was analysed with PAUP Version 3.1.1 on a Power Macintosh 7500/100 using the same heuristic search settings as detailed by Ruta (in press).

The analysis yielded a single tree (length = 230 steps; consistency index excluding uninformative characters = 0.456; retention index = 0.68; rescaled consistency index = 0.322) (Fig. 15). Major differences between this tree and the 3 equally parsimonious solutions found by Ruta (in press) are: 1) *Barrandeocarpus jaekeli* Ubaghs, 1979 and *B. norvegicus* Craske & Jefferies, 1989 are sister taxa and, together, form the sister-group of *Ateleocystites guttenbergensis* Kolata & Jollie, 1982; 2) *Kierocystis inserta* Parsley, 1991 and *Diamphidiocystis drepanon* Kolata & Guensburg, 1979 are successively more closely related to the remaining ingroup taxa.

Protocytidium occupies an intermediate position between *Enoploura popei* Caster, 1952 and the Allanicytidiidae as defined by Haude (1995) and Ruta (in press), thus confirming the transitional nature of several of its features. The following characters, all showing state change 0-1 numbered in the same order as they appear in the data matrix (Ruta in press) and accompanied by their consistency index (ci) values, support the sister-group relationship between *Protocytidium* and the Allanicytidiidae under the accelerated character-state transformation (character changes are placed as close to the root of the tree as possible, thus emphasising reversals): 21 (ci=1), plate MOP longer than each of the 2 plates LOP; 30 (ci=0.333), spine length greater than

Plating of the convex side of *Occultocystis* differs from that of other allanicytidiids in several details. The transition from this genus to more derived allanicytidiids was probably characterised by the disappearance of the median element of the distalmost transverse row and by elongation of C21 both distally and proximally.

The evolutionary history of more derived allanicytidiids is characterised by remarkably few character changes, most of which pertain to general proportions and relative size of plates of convex surface, skeletal sculpture and appendage morphology (Ruta & Theron, 1997; Ruta & Jell, 1999c; Ruta, in press).

PHYLOGENETIC ANALYSIS

Data from a study of interrelationships of the anomalocystitid mitrates (Ruta, in press) are used

length of distal margin of plano-concave surface; 87 (c_i=0.25), 3 plates along distalmost margin of convex surface; 90 (c_i=1), interior of distal margin of convex surface with transverse thickening with asymmetrical cross-section; 97 (c_i=1), distal styloid blade inclined proximally; 99 (c_i=0.25), a sharp, longitudinal keel on external surface of styloid; 102 (c_i=1), proximal styloid blade semicircular in outline. With the exception of characters 30, 87 and 99, the other characters are uniquely derived features of the clade (*Protocytidium elliottae* + remaining Allanicytidiidae). When the delayed character-state transformation is used (character changes are placed as far from the root of the tree as possible, thus emphasising parallelisms), the clade comprising *Protocytidium elliottae* and the remaining Allanicytidiidae is supported by state changes relative to characters 21, 30, 97, 102 as well as by character 53 (c_i=0.25), absence of overlapping elements on convex surface. From this pattern of character distribution, it is possible to highlight the major changes during allanicytidiid evolution.

Modifications of the plano-concave surface include: reduction in size and subsequent loss of B; proximo-distal elongation of A and subsequent interposition of it between C and left lateral marginal DLM, ILM and PLM; narrowing and acquisition of oblique orientation of right and left LOP, which became wedged between MOP and right and left DLM, respectively; widening of MOP; acquisition of flexible articulation between orifice plates and adjacent plates of plano-concave surface.

Modifications of the convex surface include: reduction of distal row of plates from 5 to 3 to 2 elements; great expansion of C21; arrangement of marginal plates in 4 sets of paired elements surrounding C21; projection of most distal pair of plates beyond distal margins of LOP and MOP.

Modifications of the appendage include: reduction in number of tetramerous rings; acquisition of semicircular outline of free margin of proximal styloid blade; proximally recumbent position of distal styloid blade; lateral ear-like projections of distal blade.

CONCLUSIONS

The diverse mitrate fauna of Australasia is enriched by addition of the latest Ordovician anomalocystitid *Protocytidium elliottae*. Spine morphology, external stereom texture and skeletal configuration of body plates distinguish this mitrate from other anomalocystitids. Character analysis indicates that *Protocytidium* is the most primitive member of the Allanicytidiidae. Character distribution patterns and comparison of this genus with *Enoploura* and *Occultocystis* suggest several skeletal modifications in evolution of the allanicytidiids including: 1) simplification of the convex surface plating through loss of plates; 2) modification of the orifice plates to form a flexibly articulated structure; 3) increase in the degree of bilateral symmetry of the body; 4) loss of plate B; 5) proximo-distal elongation of plate A; and 6) lateral expansions of distal styloid blade.

ACKNOWLEDGEMENTS

LITERATURE CITED

CASTER, K.E. 1952. Concerning *Enoploura* of the Upper Ordovician and its relation to other carpoid Echinodermata. Bulletins of American Paleontology 34: 1-47.

1956. A Devonian placocystoid echinoderm from Paraná, Brazil. Paleontologia do Paraná (Centennial Volume): 137-148.

1983. A new Silurian carpoid echinoderm from Tasmania and a revision of the Allanicytidiidae. Alcheringa 7: 321-335.

CASTER, K.E. & GILL, E.D. 1967. Family Allanicytidiidae, new family. Pp. S561-S564. In: Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas: New York).

CRASKE, A.J. & JEFFERIES, R.P.S. 1989. A new mitrate from the Upper Ordovician of Norway, and a new approach to subdividing a plesion. Palaeontology 32: 69-99.

DEHM, R. 1932. Cystoideen aus dem rheinischen Unterdevons. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie. Beilage-Band, Abteilung A 9: 63-93.

GILL, E.D. & CASTER, K.E. 1960. Carpoid echinoderms from the Silurian and Devonian of Australia. Bulletins of American Paleontology 41: 5-71.

HALL, J. 1858. Scientific intelligence, II. geology. 4. Crinoids of New York. American Journal of Science and Arts 25: 277-279.

HAUDE, R. 1995. Echinodermen aus dem Unter-Devon der argentinischen Präkordillere. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 197: 37-86.

JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. Paläontologische Zeitschrift 3: 1-128.

KOLATA, D.R. & GUENSBURG, T.E. 1979. *Diamphidiocystis*, a new mitrate carpoid from the Cincinnatian (Upper Ordovician) Maquoketa Group in southern Illinois. Journal of Paleontology 53: 1121-1135.

KOLATA, D.R. & JOLLIE, M. 1982. Anomalocystitid mitrates (Stylophora, Echinodermata) from the Champlainian (Middle Ordovician) Guttenberg Formation of the Upper Mississippi Valley Region. Journal of Paleontology 56: 531-565.

KONINCK, M.L. de. 1869. Sur quelques Echinodermes remarquables des terrains paléozoiques. Bulletin de l'Academie Royale des Sciences Belgique 28: 544-552.

PARSLEY, R.L. 1991. Review of selected North American mitrate stylophorans (Homalozoa: Echinodermata), Bulletins of American Paleontology 100: 5-57.

PHILIP, G.M. 1981. *Notocarpos garratti* gen. et sp. nov., a new Silurian mitrate carpoid from Victoria. Alcheringa 5: 29-38.

REED, F.R.C. 1925. Revision of the fauna of the Bokkeveld beds. Annals of the South African Museum 22: 27-226.

ROZHNOV, S.V. 1990. New representatives of the class Stylophora (Echinodermata). Paleontological Journal 24: 34-45.

RUTA, M. in press. A cladistic analysis of the anomalocystitid mitrates. The Zoological Journal of the Linnean Society.

RUTA, M. & BARTELS, C. 1998. A redescription of the anomalocystitid mitrate *Rhenocystis latipedunculata* from the Lower Devonian of Germany. Palaeontology 41: 771-806.

RUTA, M. & JELL, P. A. 1999a. *Adoketocarpus* gen. nov., a mitrate from the Ludlovian Kilmore Siltstone and Lochkovian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 377-398.

    1999b. Two new anomalocystitid mitrates from the Lower Devonian Humevale Formation of central Victoria. Memoirs of the Queensland Museum 43: 399-422.

    1999c. Revision of Silurian and Devonian Allanicytidiidae (Anomalocystitida, Mitrata) from southeastern Australia, Tasmania and New Zealand. Memoirs of the Queensland Museum 43: 431-451.

RUTA, M. & THERON, J.N. 1997. Two Devonian mitrates from South Africa. Palaeontology 40: 201-243.

UBAGHS, G. 1967. Stylophora. Pp. S496-S565. In: Moore, R.C. (ed.) Treatise on invertebrate paleontology. Part S. Echinodermata 1(2). (Geological Society of America & University of Kansas: New York).

    1979. Trois Mitrata (Echinodermata: Stylophora) nouveaux de l'Ordovicien de Tchécoslovaquie. Paläontologische Zeitschrift 53: 98-119.

VANDENBERG, A.H.M. 1992. Kilmore 1:50,000 map and geological report. Geological Survey of Victoria Report 91: 1-86, + map.

VANDENBERG, A.H.M., RICKARDS, R.B. & HOLLOWAY, D.J. 1984. The Ordovician-Silurian boundary at Darraweit Guim, central Victoria. Alcheringa 8: 1-22.

WETHERBY, A.G. 1879. Description of a new family and genus of Lower Silurian Crustacea. Journal of the Cincinnati Society of Natural History 1: 162-166.

APPENDIX

Through this and the following 4 papers by the same authors reference is made to a system of plate nomenclature proposed in a paper by the senior author that remains in press with The Zoological Journal of the Linnean Society of London (Ruta, in press). To facilitate the use of this nomenclature in the papers published in this volume a key to that plate notation is provided below.

Plating of the convex surface is shown on the lefthand diagram and of the plano-concave surface on the right. The convex surface is based on the maximum regular plating known which occurs in the South African *Bokkeveldia oosthuizeni* Ruta & Theron, 1997. This terminology has been developed to avoid entirely any implied interpretation of orientation or function and although no thanks may be forthcoming for introducing another terminology in an already contentious area we believe use of

terminology which removes all interpretation is desirable and should be of benefit to the enduring arguments surrounding these animals.

The following abbreviations are employed on the figure:- On the convex surface 'c' prefix is for convex and equates to the 'v' for ventral used by Ruta & Theron (1997).

On the plano-concave surface

PM = proximal marginal plates
PLM= proximal lateral marginal plates
ILM= intermediate lateral marginal plates
DLM = distal lateral marginal plates
LOP = lateral orifice plates
MOP = median orifice plate
Central plates:-
A = anomalocystid plate
B = second asymmetrical plate of some genera
C = largest central plate